Ann. Natal Mus. Vol. 37 Pages 183–189 Pietermaritzburg October, 1996

Viviparous adaptations in the acalyptrate genera *Pachylophus* (Chloropidae) and *Cyrtona* (Curtonotidae) (Diptera: Schizophora)

by

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ABSTRACT

The female reproductive system of *Pachylophus proximus* Adams (Chloropidae) is described, with additional notes concerning two other species of the genus. In these species one ovary is atrophied, and the other is reduced to a single ovariole. In addition, one large egg is retained in the terminal part of the reproductive tract (uterus) until a fully developed first instar larva develops within the chorion. The female reproductive system of several undescribed species of *Cyrtona* Séguy (Curtonotidae), with its brood pouches, is described and illustrated. The brood pouch retains a number of eggs after fertilisation, and the first instar larvae are kept there until deposition.

INTRODUCTION

Forms of viviparity are common in calyptrate Diptera, but in contrast acalyptrates show few such examples. D. K. McAlpine (1990) cites the findings of Lopes (1935) concerning the presence of small first instar larvae in the female abdomen of *Lochmostylia* Hendel (Ctenostylidae), adding his own observation of a similar condition in *Tauroscypson* Curran of the same family. Hennig (1971) recorded the heleomyzid *Dichromyia sanguiniceps* (Wiedemann) as another viviparous or ovoviviparous acalyptrate. J. F. McAlpine (1989) mentions finding a large larva in the oviduct of *Nothybus longithorax* Rondani (Nothybidae). In the Chloropidae, *Pachylophus beckeri* Curran was recorded as depositing first instar larvae singly on rice plants (Moyal 1982). Further notes on the occurrence of first instar larvae in females of species of *Pachylophus* Loew were added by Spencer (1985). Possibly all these instances are to be regarded as ovoviviparity; that is, the fertilised egg is retained for a period in the reproductive tract, and embryonation proceeds up to the formation of a first instar larva, but this remains within the chorion until the time of deposition.

Anatomical details of the female reproductive system in three Zambian species of *Pachylophus* Loew (Curtonotidae) are discussed below, revealing the extreme internal modifications undergone in females. A striking instance of viviparity is also reported below for some undescribed Zimbabwean species of *Cyrtona* (Curtonotidae). These *Cyrtona* species are multilarviparous and deposit a number of small first instar larvae; this is in contrast to the three *Pachylophus* species studied, which are unilarviparous and deposit an exceptionally large first instar larva.

METHODS AND COLLECTING SITES

All specimens were dissected under a dissecting microscope and the preparations drawn with the help of a squared eyepiece. Cleared microscope preparations were

made of the female reproductive system of a *Cyrtona* species and of a first instar larva of that genus.

Adults of *Pachylophus proximus* Adams were collected in the suburbs of Lusaka, Zambia, by sweeping in an open garden site. Adults of *P. flavipes* Lamb and *P. femoratus* (Johnson) were collected from grassy areas in farmland, especially in a mixed orchard area, in Lusaka East.

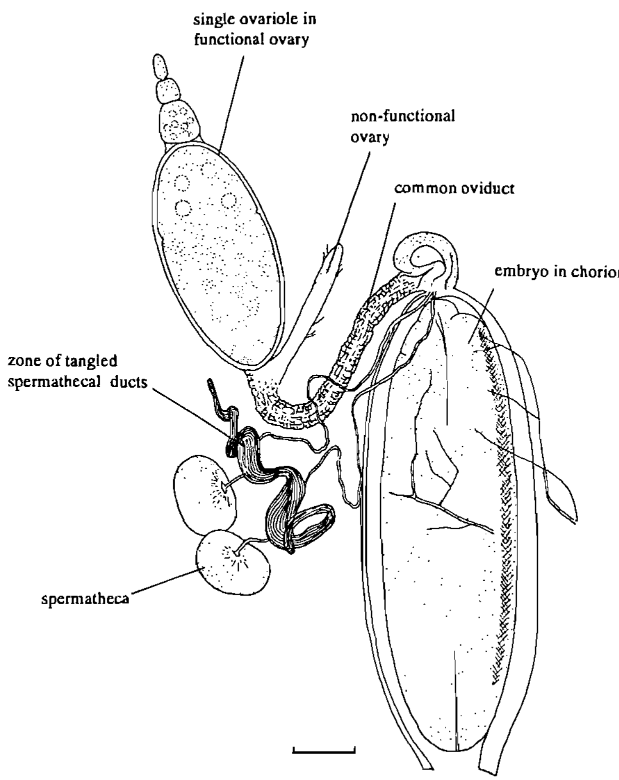

Fig. 1. Female reproductive system of *Pachylophus proximus* Adams (Chloropidae), as seen in dissection. [Scale bar = 200μm.]

The field observations of *Cyrtona* Séguy were undertaken at various localities in northern Zimbabwe between July 1990 and December 1991. Several species near to *C. albomacula* (Curran) were present, and most, perhaps all, are undescribed. Collecting sites lay within the catchment areas of the Manyame (Hunyani) River and the Mazowe River, both of which run generally north and northeast from plateau areas around Harare, to the Zambezi River.

ADAPTATIONS TO THE FEMALE REPRODUCTIVE SYSTEM OF *PACHYLOPHUS* (CHLOROPIDAE)

Pachylophus proximus Adams

There is only one functional ovary (probably the left one), but the action of

dissection alters the relative position of organs, sometimes making such an identification uncertain. The other ovary is atrophied to the extent that only the stump of the ovarian duct is visible, and this leads to a blind end which has some tracheae supplying it (Fig. 1). No ova have been detected in this structure (15 specimens dissected).

The functioning ovary consists of a single ovariole, on the left side of the abdomen. There was no sign of other ovarioles, either functional or vestigial. The ovariole contained a large ovum in all but 2 of the 15 specimens dissected; the exceptional cases had apparently just ovulated, and a relatively immature ovum above a loose, extensive follicular relic was found in the ovariole. Likewise, in other cases in which a fairly recently ovulated egg was present in the uterus, there was a compacting follicular relic visible in the intact ovariole, below the largest developing ovum.

The egg/embryo retained in the uterus always lies along virtually the entire right side of the abdomen. The mature egg at ovulation measures about 1.45 mm, nearly half the length of the adult female. While no movement of ova have been observed, some inferences concerning the sequence of actions occurring during ovulation can be derived from observations made in dissections. What appeared to be a freshly ovulated egg was found in the uterus of two specimens. The area of the ovariole from which the egg was shed could easily be identified, and the follicular coat had not yet contracted. Specimens have been found with rather contracted, rounded follicular relics in the ovariole, and this seems to represent the next stage. When the process of embryonic development has proceeded to the point at which the larval mouthparts can be seen, the ovum awaiting ovulation is about as large as the embryonated egg in the uterus.

There cannot be sufficient room within the abdomen for the ovulating egg to follow the course of the oviduct as it appears in the resting state. By such a mechanism, at some stage, the ovulating egg would have to be positioned across the abdomen, which is anatomically impossible. Rather, while the egg is being assisted with its passage into the uterus by the contortions of the oviduct, it retains a mainly anteroposterior orientation. A change in position of the ovulating egg from the left to right side of the abdomen results from these events, and space on the left side is made available for further growth of the next ovum.

There are two spermathecae. In dissections of fresh material, the spermathecae are white with a rotund appearance as in Fig. 1. The lumen of the spermatheca is minute, and the majority of structures seen in fresh material are composed of secretory cells.

The spermathecal ducts arise as two narrow tubes at the usual site. They are long, and before reaching the spermathecae become entangled in a specialised area which possibly has a sperm-storage function. The precise anatomical relationships in this area have not been resolved. Both spermathecal ducts contribute to the zone of highly convoluted tubes.

No accessory glands can be seen in dissections, and probably there are none.

Pachylophus femoratus (Johnson)

This species has not been studied in as much detail as the other two, as the female reproductive system was immature during the period of observation (April to May). Nevertheless, dissections showed the presence of only one ovariole.

Pachylophus flavipes (Lamb)

In this species the female reproductive system is similar to that of *P. proximus*. There is only one functional ovary, and this contains only one ovariole. However, the apical part of this ovariole is constrained by membrane so that the smaller ova and the germarium are held tightly together. The various parts have been carefully dissected to display their anatomical relations, and this confirms the presence of only one ovariole.

ADAPTATIONS IN *CYRTONA* SPECIES (CURTONOTIDAE): THE FEMALE REPRODUCTIVE SYSTEM AND SEASONAL CHANGES

In Zimbabwe, from July to early October, *Cyrtona* ovaries remain in an undeveloped state. By early November, a season of hot sunny days interspersed with cooler stormy periods, the ovaries develop large ova (Fig. 2a). In one species 20–25 ovarioles per ovary were found. Mating behaviour has not been observed, but presumably after mating the mature eggs are all passed into a brood pouch (Fig. 2b). Newly ovulated eggs are stacked within the brood pouch. As embryonation continues, the packing becomes more irregular (Fig. 2c). Later the eggs develop *in situ* into first instar larvae. Females may be found with variable numbers of such larvae within the brood pouch, suggesting that the larvae are deposited one or a few at a time, rather than all at once. Gravid females captured in the field and confined to

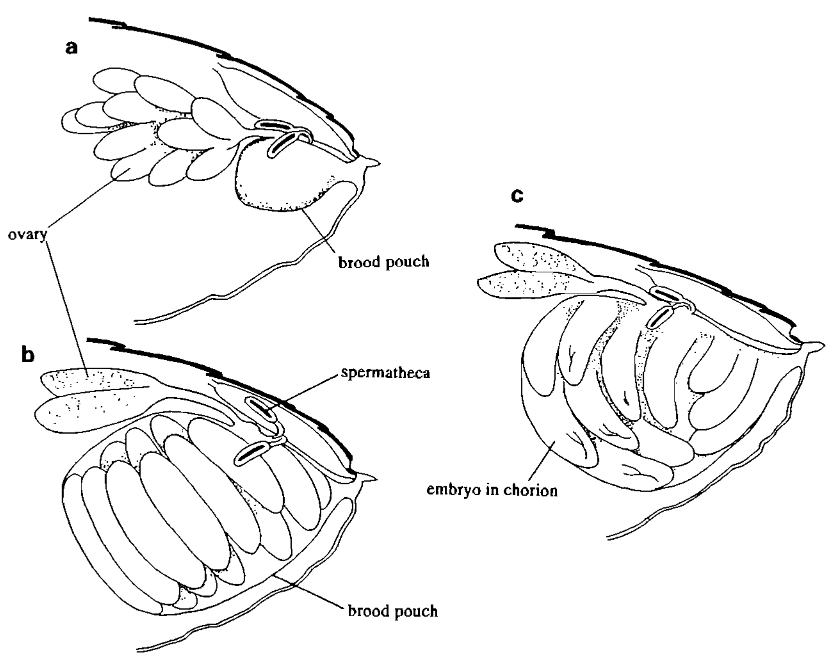

Fig. 2. Female reproductive system of a *Cyrtona* species (near *C. albomacula* (Curran)), showing passage of mature eggs into the brood pouch, and the commencement of their embryonic development there: (a) reproductive system with partially developed eggs in ovaries, and brood pouch empty; (b) eggs passed into brood pouch, and ovaries exhausted; (c) developing embryos within the brood pouch.

a specimen tube for transport back to the laboratory, often deposited several active larvae within the tube in that short time (about an hour). When dissected, such females were usually found to have one to several larvae remaining within the brood pouch (Fig. 3). Females with eggs or larvae in the brood pouch have small ovaries, but can have partially developed ova in the ovarioles, so that presumably more than one ovulation cycle is possible.

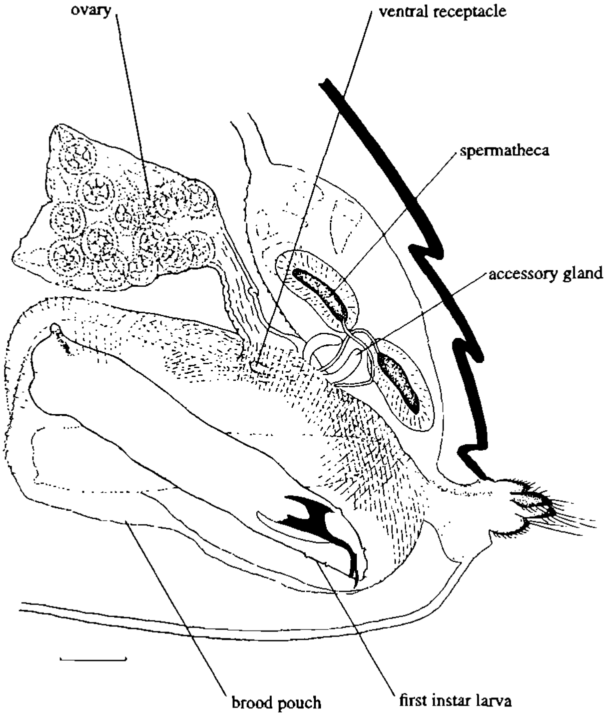

Fig. 3. Female reproductive system of a *Cyrtona* species (near *C. albomacula* (Curran)), showing first instar larvae within brood pouch. It is not known if the chorion is retained by this late stage. [Scale bar = 100μm.]

The brood pouch itself is a thin-walled muscular bag projecting anteroventrally from the reproductive tract immediately posterior to the junction with the spermathecal ducts. During the period when the ovaries are quiescent, the brood pouch walls are apparently folded, and the structure is relatively inconspicuous. In females with maturing ova still in the ovaries, the brood pouch is rather thicker walled, and contains a pale yellow fluid. After ovulation, the eggs fill out the brood pouch so that the latter occupies about half the extent of the abdomen, or even more. As the larvae are deposited, the space taken up by the brood pouch and its contents lessens, and the walls of the pouch appear more opaque.

In life, the first instar larva is about 0.6 mm long. The posterior spiracles project

momentarily during the locomotory rhythm. Specimens prepared for microscopy show the posterior spiracles raised on small rounded prominences. Later larval stages have not been observed, and the larval substrate is unknown.

The brood pouch is present as an anteroventral diverticulum of the reproductive tract, at a point posterior to the junction with the spermathecal ducts, as described above. It is easy to overlook this structure if females are examined out of season, when the ovaries are undeveloped.

In the species studied, the two spermathecae are tubular. There is a small ventral receptacle positioned near the genital papilla; it is about one-third the length of the spermathecae, and about the same width. It is slightly curved, and has secretory cells as in the spermathecae. The female accessory glands are small but well formed in the specimens examined.

DISCUSSION

The genus *Pachylophus* shows the most extreme reduction of ovariole number possible. Great reduction of ovariole number has occurred repeatedly in Diptera. It is a reasonable assumption that it occurs when offspring survival is enhanced by the adult female directing its nutritional resources into very few individual eggs, rather than into batches of numerous smaller eggs.

Well known cases of ovarian reduction include those seen in Hippoboscidae and Glossinidae. The hippoboscid *Melophagus ovinus* (Linnaeus) was shown to have two ovarioles in each of the two ovaries, with each ovary and each ovariole taking turns to produce the rather large egg that lodges in the uterus to the completion of all larval instars (Pratt 1899). *Glossina* Wiedemann (Glossinidae) was long thought to have a single ovariole in each of the ovaries (Minchin 1905), but Saunders (1960) showed that a system operates similar to that in *Melophagus* Latreille.

Great reduction in ovariole number occurs in other unrelated species of Diptera (Ferrar 1987). For instance, species of *Dyscritomyia* Grimshaw (Calliphoridae) from Hawaii have been found to have two ovarioles per ovary (Pollock 1974). In some species (e.g. Glossinidae-Hippoboscidae) there has been a specialisation of the reproductive tract, so that nutritive organs (modified accessory glands in the above example) are available for the sustenance of the growing larva within the female tract. The modification is in principle distinct from, and where it occurs, supplementary to ovariole number reduction, and there is no sign of it occurring in *Pachylophus proximus*. Indeed, in all dissections performed, the embryo retains the chorion around it, and accessory glands are absent in females.

The three species of *Pachylophus* studied here have a functional ovary that contains only one ovariole. The appearance of the apical part of the ovariole is somewhat different in *P. flavipes*, compared to the other two species. In *Pachylophus proximus*, each developing ovum is in line with its neighbours, and once the ovary is revealed, it is clear that only one ovariole is present, without the need for further dissection. In *P. flavipes*, as described above, some careful dissection is needed to verify that the ovary consists of one ovariole, not two. The third species studied resembles *P. proximus* in respect of the ovarian condition. It would be of interest to construct life tables for such slow-breeding Diptera. It may well be that, annually, the

innate capacity for increase in numbers is lower in *Pachylophus* species than in *Glossina* species, because of the marked breeding seasonality seen in at least some *Pachylophus* species. Normally, *Glossina* breeds all year round.

A radically different type of viviparity is shown in the little-studied curtonotid genus *Cyrtona*. Ovariole number is not reduced compared to many oviparous flies. A batch of first instar larvae resides in a special brood pouch for a time, just as numbers of larvae do in the oestrids *Oestrus* Linnaeus and *Cephenemyia* Latreille, which have the habit of depositing larvae in or near the nostrils of mammalian hosts. The female accessory glands are retained in *Cyrtona*, although they remain small and are therefore unlikely to have any special function relating to viviparity. This type of viviparity is extremely uncommon in acalyptrates, although multilarviparity is at least found in the Ctenostylidae. Knowledge of the larval substrate of *Cyrtona* would be interesting; the possibility that larvae are parasitic deserves to be investigated.

ACKNOWLEDGEMENTS

I thank Dr John Deeming for identifying the chloropid species, and for help with the chloropid literature; Dr. D. K. McAlpine for identifying *Cyrtona* to genus, and for giving assistance with the relevant literature; Dr. L. Tsacas for indicating that the *Cyrtona* species studied were undescribed; Dr. T. Muller for allowing the capture of Curtonotidae from Christon Bank Nature Reserve, Mazowe, Zimbabwe; and Mr and Mrs M. Bingham and Mr and Mrs Y. Mwale for encouraging the study of Diptera on their property in Lusaka. The input of an anonymous referee is also acknowledged.

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Date received: 23 February 1996